EUGENE S. GAFFNEY

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ABSTRACT

Miocene freshwater deposits in the Tirari Desert region of South Australia have yielded the first skull material of chelid turtles in the fossil record. Partial skulls consisting of well preserved but disarticulated elements are very similar to the Recent genus *Emydura*, hypothesized by Gaffney (1977) as one of the more plesiomorphic of the Recent chelids. Well-preserved shells, cervical vertebrae, and limb elements are also consistent with this identification.

INTRODUCTION

Side-necked turtles of the family Chelidae occur today in South America and Australia. Although they are common in South America and are the dominant continental turtle group in Australia, their fossil record is sparse, consisting of shell fragments and a few complete shells (see Warren, 1969, and references for Australia; Wieland, 1923; and Wood, 1976, for South America). The discovery of chelid skull material in Miocene deposits in South Australia by field parties under the direction of the University of California at Berkeley and the South Australian Museum marks a significant change in this situation. In the present paper I describe this skull material as well as some well-preserved postcranial specimens. In a paper currently in preparation I will review all the records of Australian fossil turtles, but because most of the chelid records consist of fragmentary material that conveys a minimum of mor-phological information, I have segregated the best-preserved chelid skulls and shells for description here. Earlier work on fossil Australian turtles will be dealt with in that paper. The taxonomic usage within Chelidae follows that of Gaffney (1977) which should be seen for skull figures and discussions of characters. Throughout this paper I include the genus *Elseya* in *Emydura*.

ABBREVIATIONS

ANATOMICAL

ang, angular	fr, frontal
art, articular	ju, jugal
bo, basioccipital	mx, maxilla
bs, basisphenoid	na, nasal
cor, coronoid	op, opisthotic
den, dentary	pa, parietal
epi, epipterygoid	pal, palatine
ex, exoccipital	pf, prefrontal

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pm, premaxilla   qu, quadrate
po. postorbital   so, supraoccipital
pr, prootic   sq, squamosal
pt, pterygoid   sur, surangular
qj, quadratojugal   vo, vomer

INSTITUTIONS

AMNH, American Museum of Natural History
UCMP, University of California, Museum of Paleon-
    tology, Berkeley

LOCALITIES

All the material described here comes from
either of two localities discovered and collected
by the University of California—South Aus-
tralian Museum field parties under the direction
of R. A. Stirton. Both localities are along the
shores of salt lakes in the Tirari Desert, east of
Lake Eyre, in the state of South Australia. The
most specific information about these localities
can be found in Stirton, Tedford, and Miller
(1961) and Stirton, Tedford, and Woodburne
(1967). More general reviews of the stratigra-
phy and faunas involved can be found in Stir-
ton, Tedford, and Woodburne (1968) and
Woodburne et al., in press.

V 5762, Turtle Quarry (fig. 1).

LOCATION: Along the southwestern edge of
Lake Palankarinna, grid coordinates 656.7–
429.5, 657428, grid zone 5, Marree sheet,
South Australia, 1:506880, Australian Army
Cartographic Company, 1942. Discovered by
R. H. Tedford, June 30, 1957.

STRATIGRAPHY: V 5762 occurs low in the
Etadunna Formation and is one of the older
vertebrate-bearing units in that formation. Stir-
ton, Tedford, and Miller (1961, fig. 4) present a
composite section of the Etadunna Formation
indicating the position of V 5762 in Unit 4.
They describe Unit 4 as "pale green, well
sorted, fine-grained quartz sand with lenses of
green argillaceous sandstone . . . 2–4 feet"
(Stirton, Tedford, and Miller, 1961, p. 52).

The dating of interior continental deposits in
Australia is difficult and the limits of the proce-
dures involved should be kept in mind. There
are no direct marine tie-ins or radiometric dates
available for the Tertiary deposits containing
the turtles described here. The two methods
currently used for ideas about age involve (1)
physical and biostratigraphic correlation with
rocks yielding pollen that can be placed directly
into standard zones and (2) biostratigraphic
(primarily mammalian) correlation with rocks
associated with or in turn correlatable with
datable volcanic rocks. Stirton, Tedford, and
Woodburne (1968) set up a biochronology for
the Australian Tertiary terrestrial deposits. At
that time they dated the Ngapakaldi Fauna of
the Etadunna Formation as "late Oligocene (or
early Miocene?)" (p. 4). Since then, pollen
samples from another site in the Etadunna For-
mation (Woodburne et al., in press) suggest a
medial Miocene age instead.

V 6213, Leaf Locality.

LOCATION: A vertebrate-bearing site along
the eastern shore of Lake Ngapakaldi (indicated
on maps in figs. 1–4, Stirton, Tedford, and
Woodburne, 1967).

STRATIGRAPHY: V 6213 occurs in the Wipa-
jiri Formation and is the type locality of the
Kutjamarpu Fauna. The Wipajiri Formation is a
stream channel cut into the Etadunna Formation
and generally yields disarticulated but not
abraded vertebrates. However, the best-pre-
served chelid shell from Australia (UCMP
77348) and the only specimen of a chelid shell
associated with other skeletal elements (UCMP
72492) comes from this formation.

Even though the Wipajiri Formation cuts
into the Etadunna Formation and is therefore
younger, the enclosed Kutjamarpu Fauna is not
thought to be very much younger than the
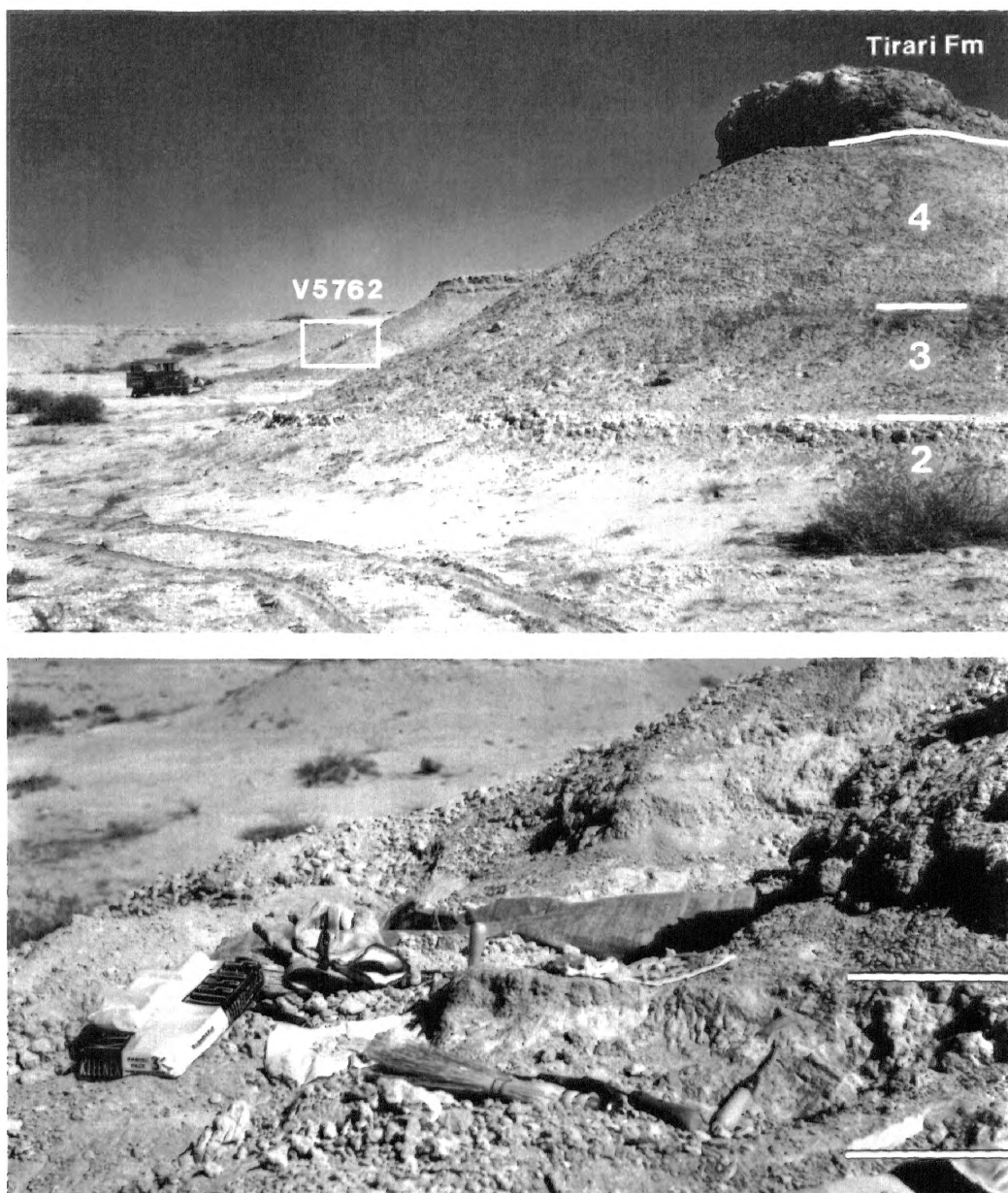Ngapakaldi Fauna of the Etadunna Formation.

FIG. 1. University of California Museum of Paleontology locality V 5762, Turtle Quarry, Lake Palankarinna, Tirari Desert, South Australia. The upper figure shows the stratigraphic units (2–4, using notation of Stirton, Tedford, and Miller 1961) of the Etadunna Formation exposed here. V 5762 (seen in the left distance) lies at the base of unit 4, a green sand and mudstone. The Plio-Pleistocene Tirari Formation unconformably lies above these units of the Etadunna Formation. The lower figure is a closeup of V 5762, the Turtle Quarry, with the awl in the lower right corner pointing to a shell fragment still *in situ*. The white lines show the vertical limit of bone distribution in the mudstone pocket. Both figures from slides taken by R. H. Tedford, July 4, 1957.

The Kutjamarpu Fauna is medial Miocene in age according to most workers (Stirton, Tedford, and Woodburne, 1968; Woodburne et al., in press).

DESCRIPTIONS

1. CRANIAL MORPHOLOGY

V 5762 has yielded nearly all of the fossil

chelid skull material presently known from Australia.[1] The skull elements occur disarticulated and mixed with other skeletal elements: vertebrae, limb bones, and shell pieces. The following list shows the number of cranial elements recovered from V 5762: 16 parietals, 12 maxillae, 9 quadrates, 9 frontals, 5 pterygoids, 5 postorbitals, 4 supraoccipitals, 3 exoccipitals, 3 squamosals, 2 basisphenoids, 1 jugal, 1 basioccipital; no premaxillae, vomers, nasals, palatines, prefrontals, quadratojugals, or lower jaws.

By attempting to articulate right and left parietals, I conclude that 13 different individuals are represented in the sample of 16 parietals (10 left, 6 right), and this gives a minimum figure for the number of individuals contributing to the total thanatocoenosis. Although the anterior half of a plastron (not seen, Tedford, notes) was found articulated, all the remaining material was disarticulated, but some of the skull elements can be re-articulated and the following partial skulls result:

UCMP 57253–frontals, parietals, postorbitals, prootics, basisphenoid, supraoccipital (figs. 3-5).

UCMP 78229–quadrates, opisthotics, exoccipitals, basioccipital, left frontal, left parietal, left prootic, left squamosal (part), right pterygoid (part) (figs. 2, 7-9)

UCMP 57056–parietals, left frontal, left postorbital.

UCMP 119937–left quadrate, left opisthotic.

UCMP 119938–right quadrate, right opisthotic.

UCMP 119939–supraoccipital, right parietal.

UCMP 119975–left parietal, left frontal.

UCMP 119993–left maxilla and left jugal.

NASAL: (Not preserved.)

PREFRONTAL: (Not preserved.)

FRONTAL: Nine frontals are available in the collection from the Etadunna Formation, in-

cluding five that articulate with other elements. Two of these are part of UCMP 57253 (figs. 3-5), a partial skull; whereas one each is in UCMP 78229 (figs. 7-8), a partial skull; UCMP 57056, a partial skull roof; and UCMP 119975, a parietal and frontal only. Thus, eight individuals are represented.

One of the important regions in chelid systematics is the morphology of the anterior portion of the skull roof. The diagnostic character of the subfamily Chelinae (Gaffney, 1977) is the anterior frontal process at least partially separating nasals. In the absence of both prefrontals and nasals in the Etadunna material, it is impossible to be certain about the presence of this character but the morphology of the Etadunna frontals is virtually identical with that in Recent *Emydura*. The anterior frontal process is well developed (figs. 2, 4, 5) and has sutural attachment areas for prefrontal and, presumably, nasal bones, although these sutural areas are not distinct from each other. The anterior frontal process of *Emydura* is quite different from that region in *Pseudemydura* and *Chelodina* (Gaffney, 1977, figs. 2, 3).

PARIETAL: The presence of 16 parietals in the V 5762 collection makes this bone the most common cranial element. Six parietals (included in specimens: UCMP 8229, 57056, 57253, and 119975) articulate with other elements.

The Etadunna parietals (figs. 3-5, 7, 8) agree closely with Recent *Emydura* parietals in that they lack the reduced lateral margins seen in the tribe Chelini *(Phrynops, Chelus, Chelodina,* and *Hydromedusa)* but have a well-developed posterolateral process that articulates with the squamosal. The fossil parietals differ from Recent *Emydura* in having a slightly less extensive posterior temporal emargination but this does not seem systematically significant to me.

JUGAL: In the subtribe Chelina *(Chelus, Chelodina,* and *Hydromedusa)*, the medial portions of the jugal and postorbital face more laterally than posteriorly, whereas other members of the Chelidae have the primitive condition in which the jugal and postorbital face more posteriorly. The single Etadunna jugal (UCMP 119993) agrees with the more primitive

[1] At the present time I am aware of the following chelid cranial material exclusive of that from V 5762: lower jaws of *Emydura* sp. from the Miocene Wipajiri Formation at V 6213; lower jaws of *Emydura* sp. from "Darling Downs" possibly from the (?) Pliocene Chinchilla Formation, and a chelid basisphenoid from the Miocene Namba Formation at Lake Pinpa. These records are dealt with in a forthcoming work.
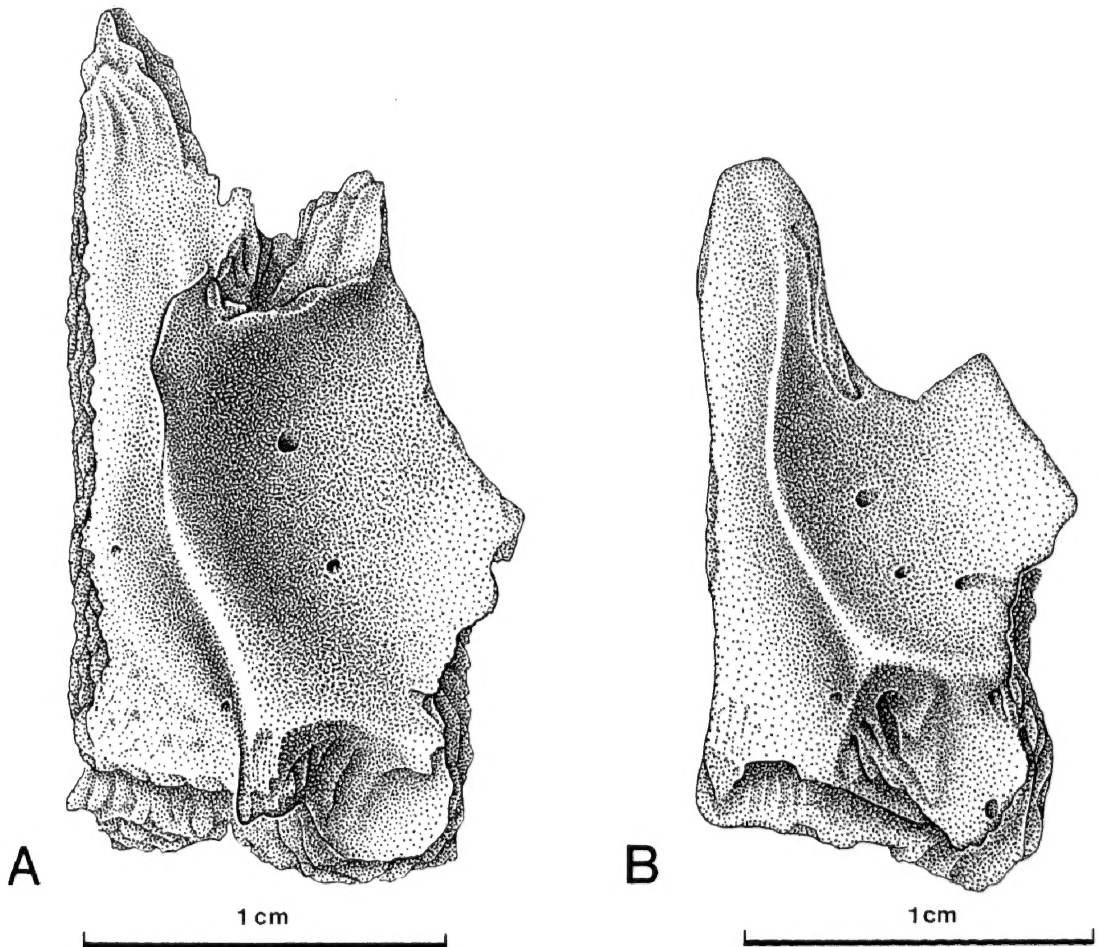
FIG. 2. *Emydura* sp., ventral views of left frontals. A, UCMP 78229 (see also figs 7 and 8); B, UCMP 119973. Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

condition found outside the Chelina, and agrees in detail with the jugal in *Emydura*.

QUADRATOJUGAL: The absence of a quadratojugal is a shared derived character for the family Chelidae. The quadrate, jugal, and parietals from V 5762, clearly show that there is no distinct sutural attachment area for a well-developed quadratojugal, and the bone was presumably absent from the skull in Etadunna chelids.

SQUAMOSAL: The morphology of the squamosal is of distinct value in chelid systematics and allows one to readily distinguish among the three Recent Australian chelids, *Emydura*, *Pseudemydura*, and *Chelodina*. The South

American chelids can also be differentiated although not as readily. The squamosal of *Pseudemydura* (Gaffney, 1977, figs. 1, 2) is large and has extensive sutural contact with the parietal anteriorly and medially and with the supraoccipital posteromedially. The squamosal of *Chelodina* has no contact with either parietal or supraoccipital, whereas in *Emydura* the squamosal has a narrow anteromedial process reaching the parietal. UCMP 119958, a nearly complete left squamosal, clearly shows the *Emydura* condition. The other two squamosals (UCMP 78229, figs. 7-8; and 119981) do not have this region preserved.

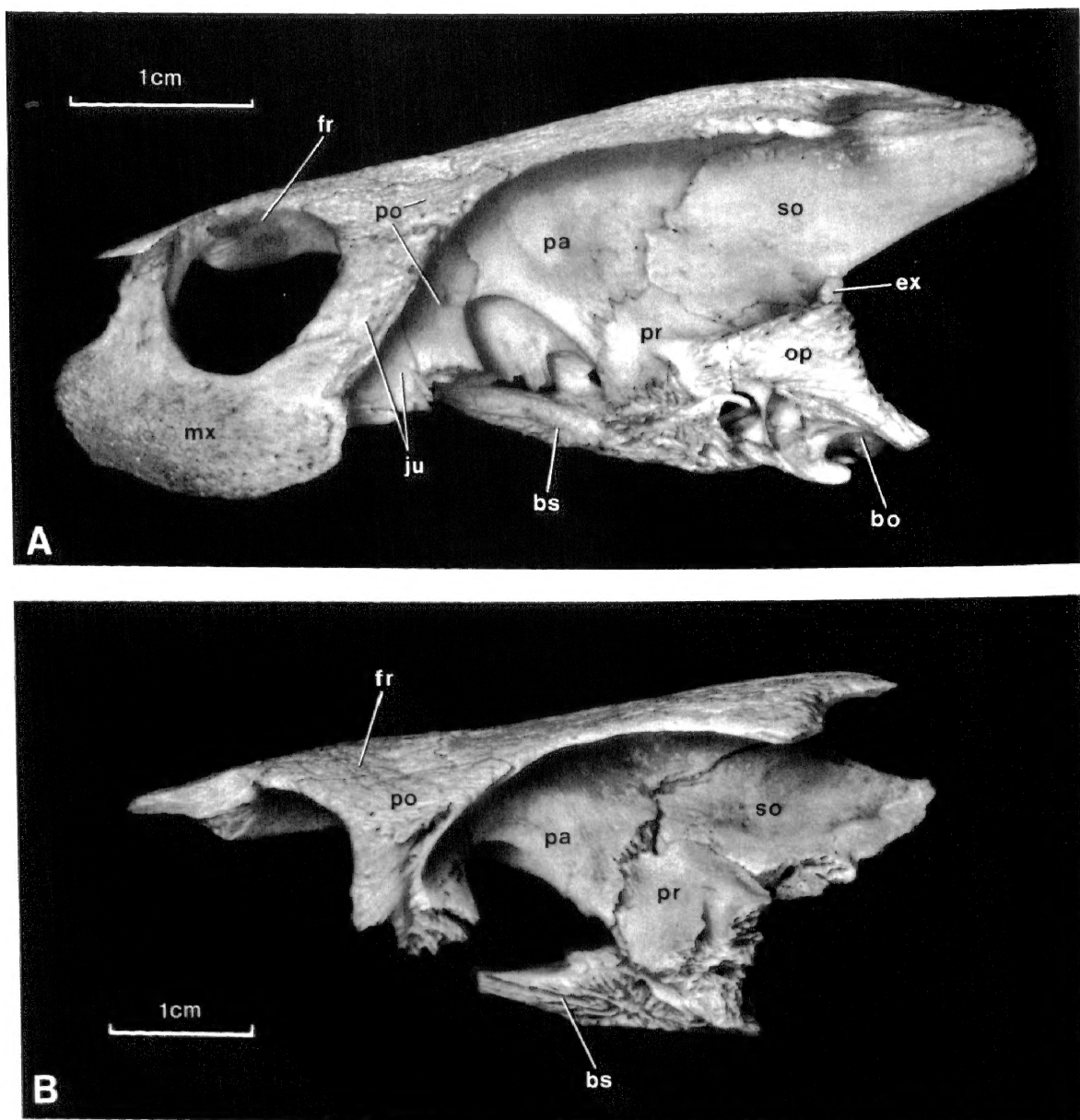POSTORBITAL: Five postorbitals are preserved

FIG. 3. Left lateral views of Recent and fossil *Emydura* skulls. A, *Emydura australis*, AMNH 108857, Recent; pterygoid, quadrate, and squamosal removed to facilitate comparisons. B, *Emydura* sp., UCMP 57253 (see also figs. 4 and 5), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

from V 5762, two of them as part of the partial skull UCMP 57253 (figs. 3-5) and one in UCMP 57056, a skull roof. All agree closely with Recent *Emydura* and differ sharply from the condition seen in the subtribe Chelina (see Jugal above).

PREMAXILLA: (Not preserved.)

MAXILLA: I did not utilize maxillary morphology for my chelid study (Gaffney, 1977) and few other authors have done so for generic level taxa. Some of the Australian taxa are subject to macrocephaly, in which the skull
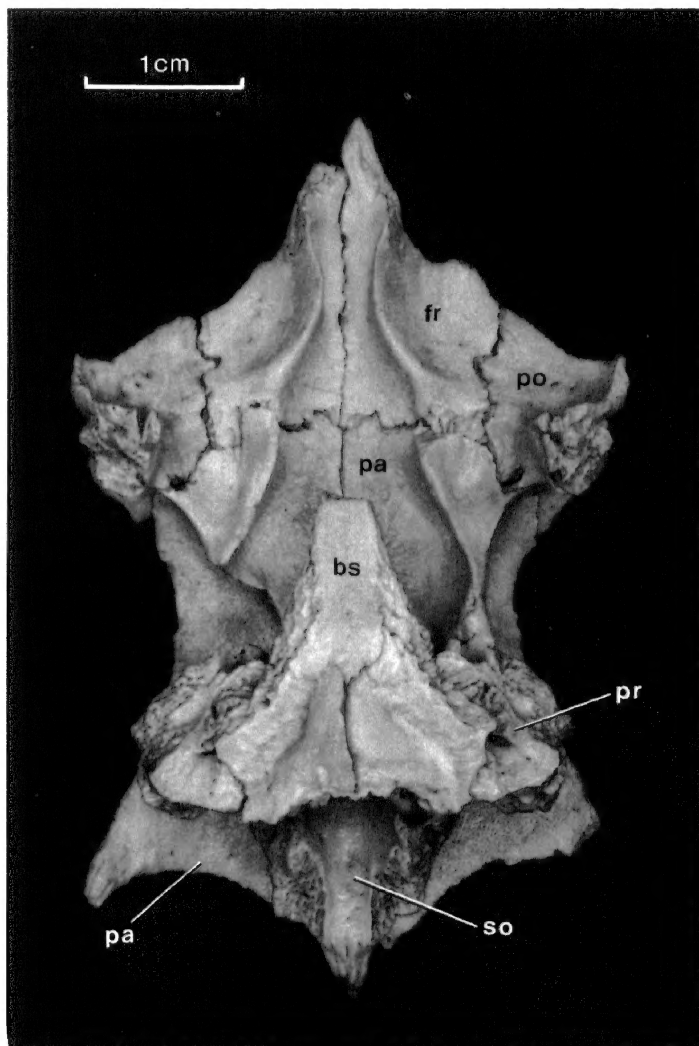
FIG. 4. *Emydura* sp., UCMP 57253, ventral views of partial skull (see also figs. 3 and 5), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

becomes particularly large and the triturating surfaces are expanded (Cogger, 1975; Dr. John Legler, pers. commun.) but the extent and systematic usefulness of this feature is not yet known. The maxilla of *Chelodina* can be differentiated from that of *Emydura* and *Pseudemydura* by the thinner triturating area and lower labial ridge in *Chelodina*. Although the medial expansion of the maxilla is usually greater in *Emydura* than in *Pseudemydura*, I do not think this distinction is consistent enough to be of value at present. Among *Emydura* spe-

cies, *Emydura australis* has been described by Goode (1967, p. 50) as having maxillae that extend far posteriorly and conceal the vomer. I have not seen specimens that agree with this description (but I have seen only one adequately identified skull of *E. australis*) and it may be due to macrocephaly. *Emydura (Elseya) dentata* is commonly characterized by the possession of a well-developed lingual ridge as opposed to the low lingual ridge of other *Emydura*, and this feature may very well be useful for distinguishing that species.
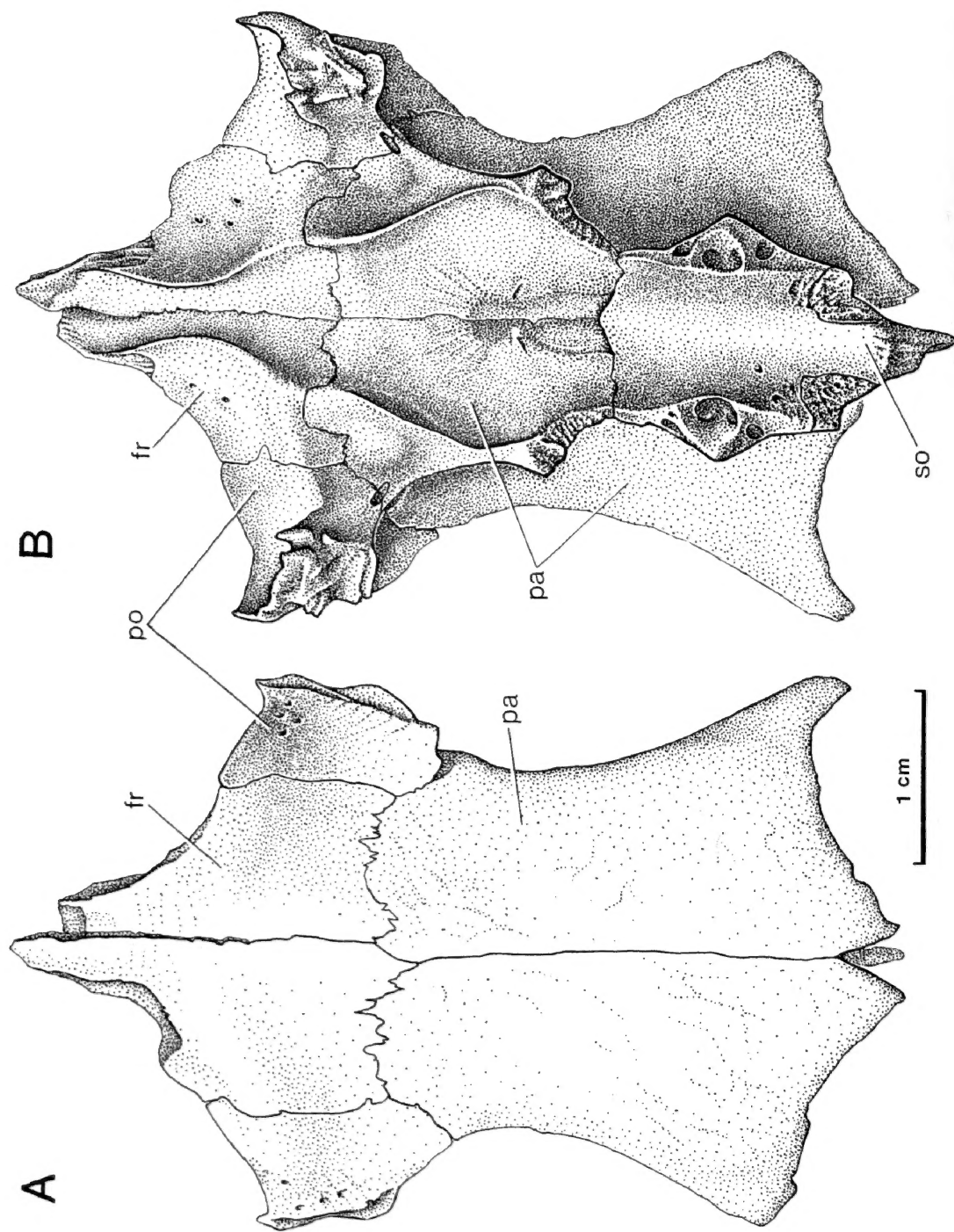
Fig. 5. *Emydura* sp., UCMP 57253. A, dorsal view; B, ventral view with basisphenoid and prootics removed, partially restored (see also figs. 3 and 4), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.
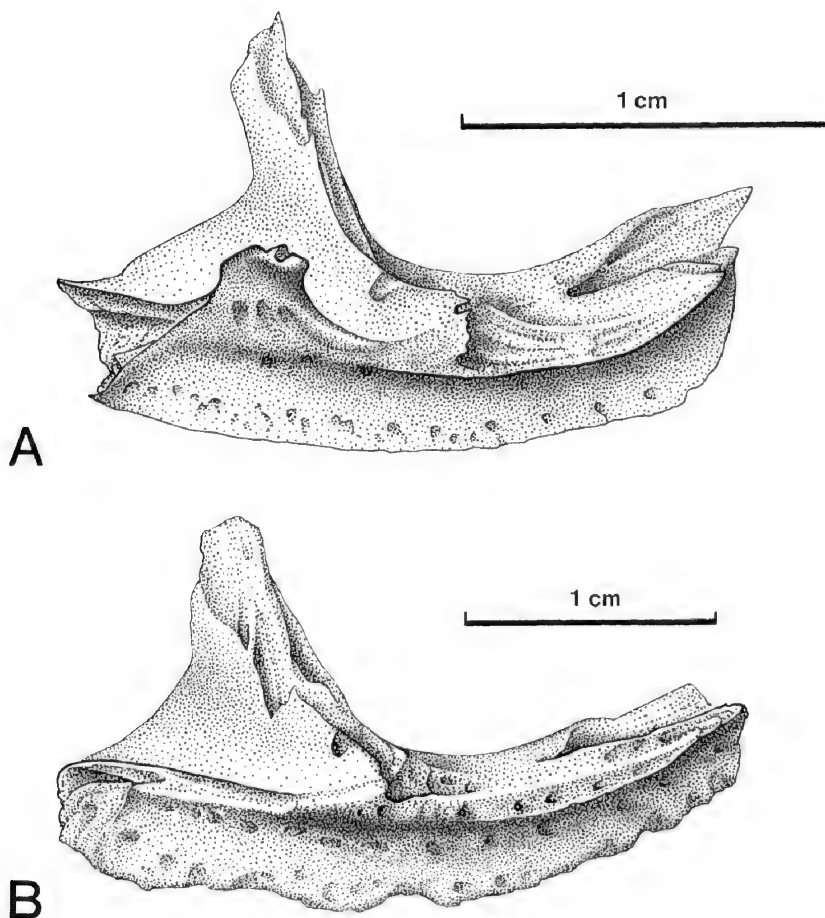
FIG. 6. Internal views of right maxillae. A, *Emydura macquarrii*, AMNH 108956 Recent. B, *Emydura* sp., UCMP 119952, Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

Although there are 12 maxillae preserved from V 5762 none is complete; all lack the thin medial process roofing part of the palate. These maxillae do not articulate with any other elements except in the case of UCMP 119993, which is a jugal and maxilla. The absence of the medial area precludes definite assignment to *Emydura* but the robust shape and detailed agreement (fig. 6) of them with the maxillae in Recent *Emydura* suggest this identification. The lingual ridge is not raised as in *Emydura dentata* and there are no indications that the triturating surface was expanded as in macrocephalic chelids.

VOMER: (Not preserved.)

PALATINE: (Not preserved.)

BASISPHENOID: Two basisphenoids (fig. 10) show no significant differences from Recent *Emydura*.

QUADRATE: Ten quadrates are in the collection, including two very well-preserved ones that articulate with the partial skull UCMP 78229 (figs. 7-8). None of these differs in any significant way from my *Emydura* material, except in size; UCMP 78229 is larger than any Recent *Emydura* skulls that I have seen. A quadrate–basisphenoid contact as seen in *Chelodina* and *Hydromedusa* is absent.

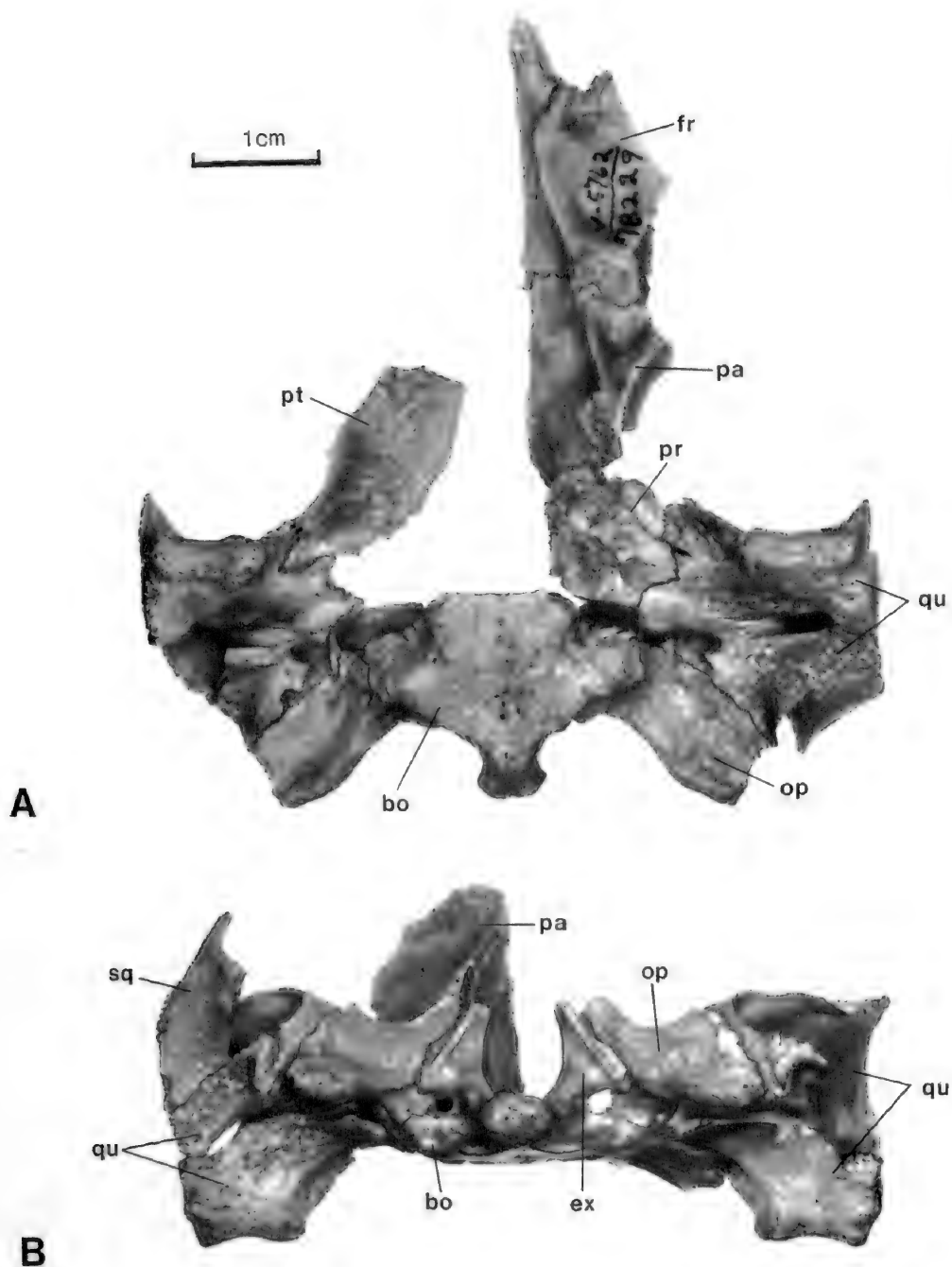PTERYGOID: Although five pterygoids are known from V 5762, none is complete. Four of

FIG. 7. A, ventral and B, occipital views of a partial skull of *Emydura* sp., UCMP 78229 (see also figs. 8 and 9), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.
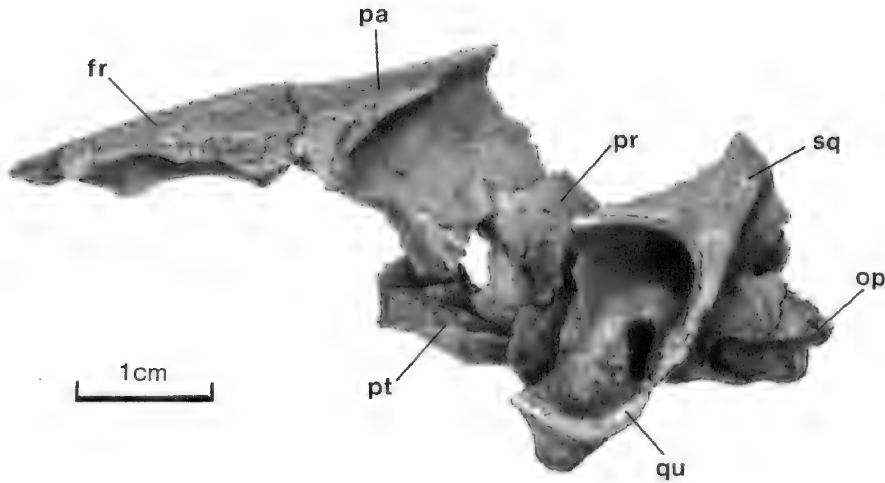
FIG. 8. Left lateral view of a partial skull of *Emydura* sp., UCMP 78229 (see also figs. 7 and 9), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

them (UCMP 119959, 119960, 119961, 119988) consist primarily of the processus trochlearis pterygoidei, whereas the fifth (UCMP 78229) is the more medial portion. Only UCMP 78229 can be articulated with other elements and it fits (somewhat tenuously) into one of the two partial skulls (figs. 7, 8).

The pterygoids of *Chelodina* and *Emydura* differ distinctly, and the Etadunna material is readily seen to be of the *Emydura* morphology. Differentiating pterygoids of *Pseudemydura* and *Emydura* is another matter, however, and I have not found any good criteria. *Pseudemydura*, some *Emydura*, and other chelids such as *Phrynops* have a small foramen between the pterygoid and prootic (see Gaffney, 1977, figs. 4, 5). This foramen is absent in UCMP 78229 but the systematic significance of this is unknown.

SUPRAOCCIPITAL: In the Etadunna material the supraoccipital (figs. 3-5) is virtually the same as in Recent *Emydura*. The crista supraoccipitalis is missing from UCMP 57253 but two others, UCMP 119942 and UCMP 119939, are also known from V 5762 and are complete.

The last two show the crista developed as in Recent *Emydura*. The largest (UCMP 119939) has a thickened posterior edge as in large Recent *Emydura*.

There are two useful diagnostic features of the supraoccipital: the extent of the exoccipital suture and the contribution of the supraoccipital to the skull roof. All four supraoccipital specimens show that the exoccipitals have the primitive condition for chelids, namely that they either do not or almost meet medially above the foramen magnum. Medial contact of the exoccipital is a derived character for the infrafamily Chelodd (See Gaffney, 1977, p. 17, fig. 6). Also, in the few examples of *Pseudemydura* available, the exoccipitals are much closer than in *Emydura*. The Etadunna supraoccipitals and the exoccipitals of UCMP 78229 (see below) agree in this feature.

EXOCCIPITALS: The medial contact of the exoccipitals dorsal to the foramen magnum is an important derived character for the infrafamily Chelodd (Gaffney, 1977), which consists of *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa*. It is fortunate that an articulated
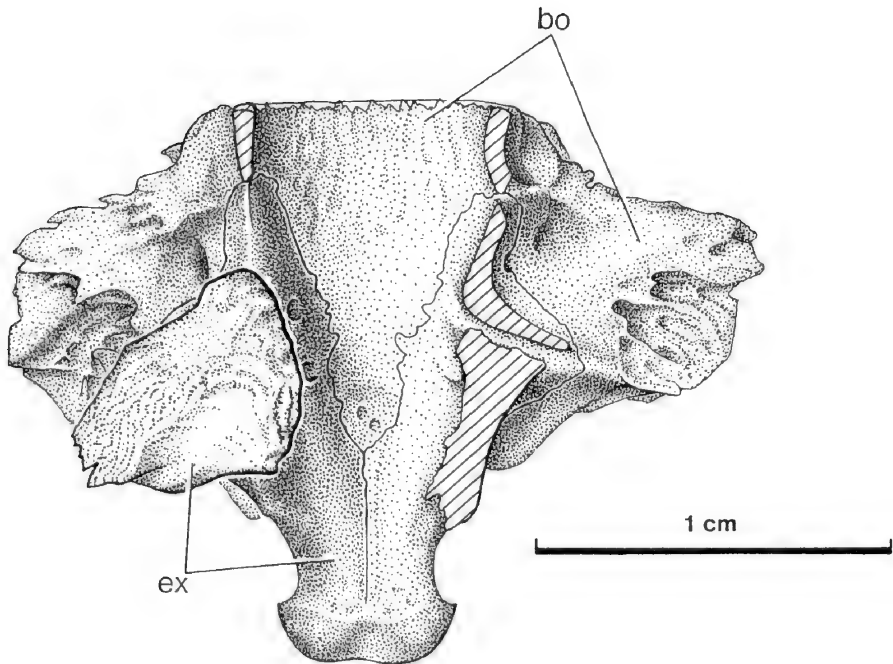
Fig. 9. Dorsal view of basioccipital and both exoccipitals with portions of right exoccipital removed to show foramina. *Emydura* sp., UCMP 78229 (see also figs. 7 and 8), Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

pair of nearly perfect exoccipitals and a basioccipital are available from V 5762. This specimen (UCMP 78229, figs. 7-9) clearly shows that the exoccipitals do not meet medially above the foramen magnum and are in fact in the condition I would consider primitive for turtles. The known supraoccipitals are in agreement with this.

The right exoccipital of UCMP 78229 was broken through its base and, although the broken piece was located, it was drawn (fig. 9) with the piece removed in order to show the anteriormost foramen nervi hypoglossi and other details normally obscured by the dorsal portion of the exoccipital.

UCMP 119945 is a disarticulated right exoccipital that agrees closely with UCMP 78229. There are no significant differences between these and the exoccipital in *Emydura*.

BASIOCCIPITAL: The only basioccipital from V 5762 is in the partial skull, UCMP 78229 (figs. 7-9). In *Emydura* this bone is distinguishable from *Chelodina* because in the latter

the condyle is drawn out more, and the area around the foramen jugulare posterius is developed into a short canal which is absent in *Emydura*. The Etadunna basioccipital agrees with *Emydura* in these features. As far as I can tell, however, the basioccipital is the same in *Pseudemydura* and *Emydura*.

PROOTIC: Both prootics are preserved in UCMP 57253 (figs. 3, 4), one in UCMP 78229 (figs. 7, 8), in addition to five disarticulated prootics. All of these have the same morphology. Among Recent *Emydura* the prootic may broadly enter the foramen nervi trigemini (Gaffney, 1975, fig. 3) or the parietal may send a process ventrally to meet the pterygoid thereby excluding the prootic from the foramen. The former condition seems most common, although I have observed the latter in many but not all specimens identified as *Emydura macquarrii*. A large series of *Emydura* that are properly identified might reveal a systematic pattern for this feature, but at present I have no reason to think that the fea-
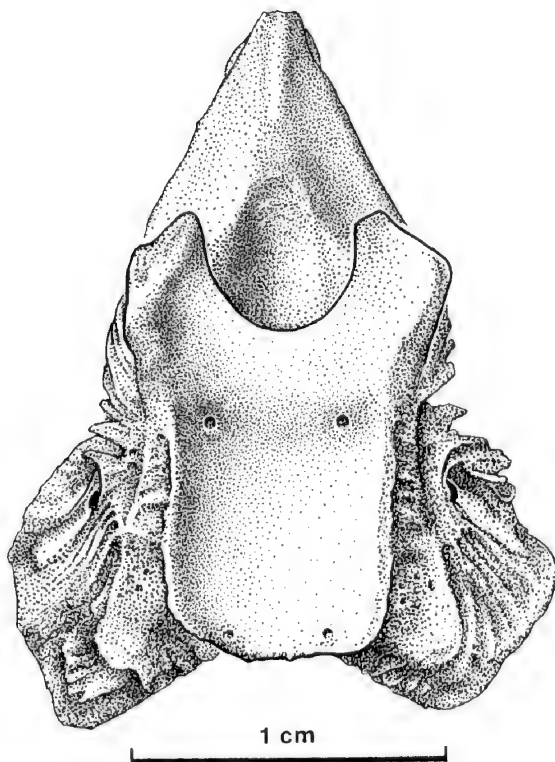
FIG. 10. Dorsal view of basisphenoid, *Emydura* sp., UCMP 119974, Etadunna Formation, Miocene, V 5762, Lake Palankarinna, South Australia.

ture is anything more than intraspecific variation. All the fossil prootics clearly show that they did not enter the foramen nervi trigemini as in the *Emydura* specimens mentioned above. Nearly all other chelids have the prootic entering the foramen (but it is very restricted in some *Phrynops*), and there is the interesting possibility that this feature may eventually allow an identification of the fossil material with some Recent species group of *Emydura*.

OPISTHOTIC: Nine opisthotics are available from V 5762 including two in the partial skull, UCMP 78229 (figs. 7, 8) and two (UCMP 119938, 119937) that fit with two quadrates (the latter pair may be from the same skull as they are right and left, but no intervening elements could be found). These opisthotics agree closely with *Emydura* as opposed to *Chelodina* but the opisthotics of all chelids are similar and not of particular systematic value.

BASISPHENOID: The basisphenoids from the Etadunna Formation (UCMP 119974 and 57253, fig. 9) agree closely with Recent *Emydura* in contrast to *Chelodina* and other members of the subtribe Chelina. These latter forms have a somewhat larger basisphenoid with distinct lateral processes that are absent in the Etadunna material.

2. SHELL MORPHOLOGY

The best-preserved fossil turtle shell from Australia is UCMP 77348 from the Miocene Wipajiri Formation, V 6213, Lake Ngapakaldi, South Australia (figs. 11-14). This specimen and another from the same locality (UCMP 72492, fig. 15, 16) are complete enough to allow useful comparisons with Recent chelids. That these specimens are members of the Chelidae is evident from the suturing of the pelvis to the shell, a derived character of Pleurodira, and the absence of mesoplastra, a derived feature of Chelidae (see Gaffney, 1975, p. 426, for more discussion of Pleurodira; Gaffney, 1977, p. 14 for Chelidae).

CARAPACE: The carapace of the Wipajiri shells agrees closely with Recent *Emydura* in all features except the relative size of the vertebral scutes. In *Pseudemydura* and *Emydura* the first vertebral scute is nearly always equal to or narrower[1] than the second vertebral scute, whereas in the infrafamily Chelodd (containing the remaining chelids) the first vertebral scute is usually wider than the second. In both Wipajiri shells the first vertebral scute is just slightly wider than the second. This seems to be a function of relatively small vertebrals 2-4. However, this character may be somewhat subject to variation. Goode's figure (1967, fig. 79) of *Emydura macquarrii* shows a specimen with the first vertebral scute just slightly wider than the second. In any case, the Wipajiri form has distinctly narrower vertebrals 2-4 than Warren's Tasmanian *Emydura* (Warren, 1969) and most Recent *Emydura*.

Both Wipajiri shells have been dorsoventrally flattened but the original outline

[1] I inadvertently stated in the Abstract of my earlier chelid paper (Gaffney, 1977, p. 1) that the first vertebral scute of the infrafamily Chelodd was narrower than the second. It should read: "First vertebral scute wider than second." The other text statements and table 3 are correct.

Fig. 11. Dorsal view of carapace, *Emydura* sp., UCMP 77348, Wipajiri Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia.

seems to have been preserved because the flattening was largely taken up by buckling along the costal-peripheral suture line. The restoration of UCMP 77348 was made under the assumption that virtually no lateral distortion took place. If this is correct, the shell outline differs from that seen in most *Emydura macquarrii* in which the posterior portion of the shell flares out and peripherals 8-10 are particularly broad (see Goode, 1967, p. 51). The other Wipajiri

FIG. 12. Dorsal view of carapace, *Emydura* sp., UCMP 77348, Wipajiri Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia. Partial restoration, bones labeled on right side, scutes labeled on left side.

shell, UCMP 72492, does flare more than UCMP 77348.

Neural bones are absent in the Wipajiri shells and other than the Tasmanian specimen described by Warren (1969), which has a single small neural, I have found no indication of neurals in any fossil Australian chelid material. This is not just negative evidence resulting

FIG. 13. Ventral view of plastron, *Emydura* sp., UCMP 77348, Wipariji Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia.

from the absence of neural bones in collections. Presence or absence of neurals can be determined from an examination of the proximal end of the vertebral surface of a costal bone for the presence of a suture for a thoracic vertebra that would normally be found on the ventral surface of a neural, if neurals were present. Although Australian chelids are sometimes characterized
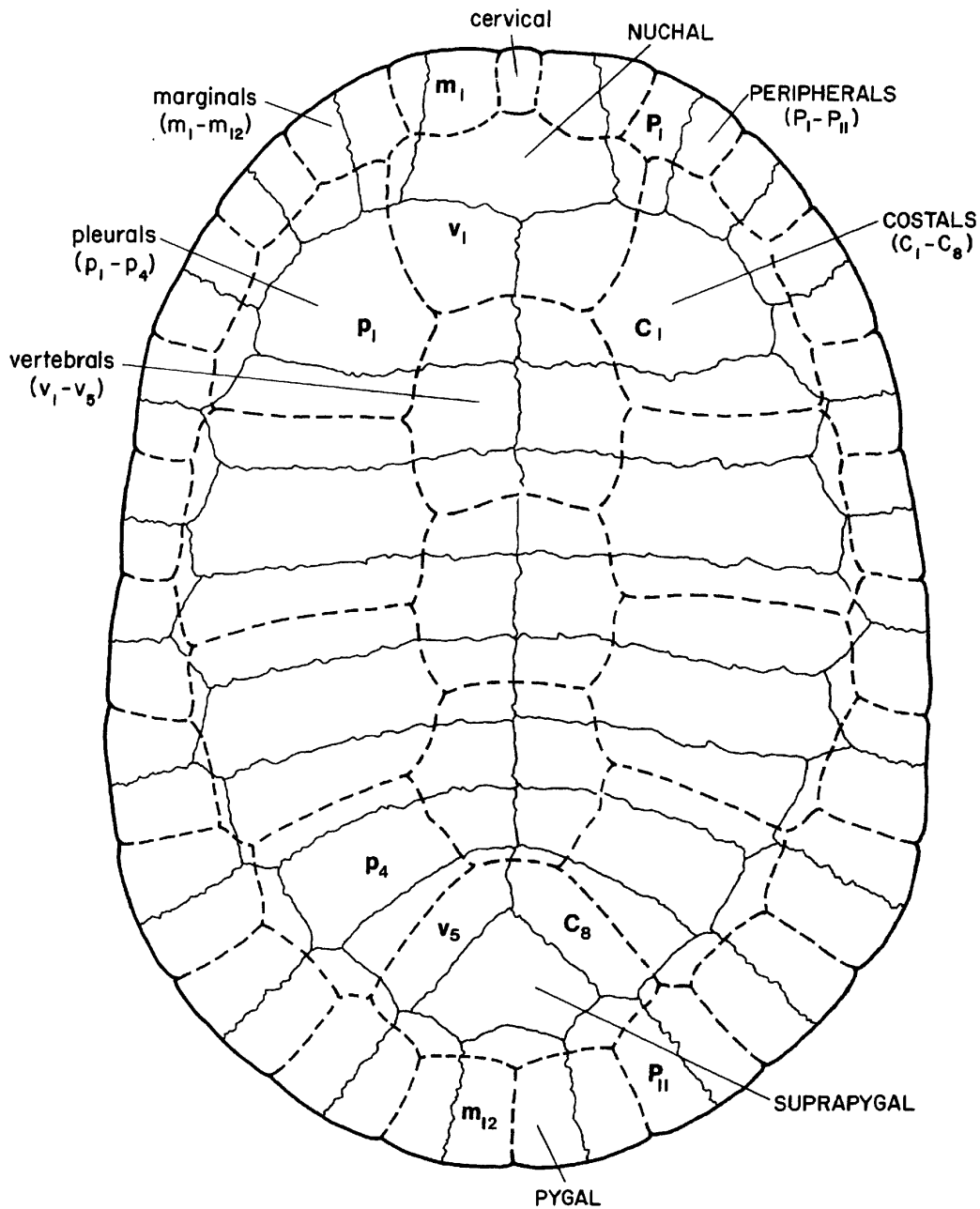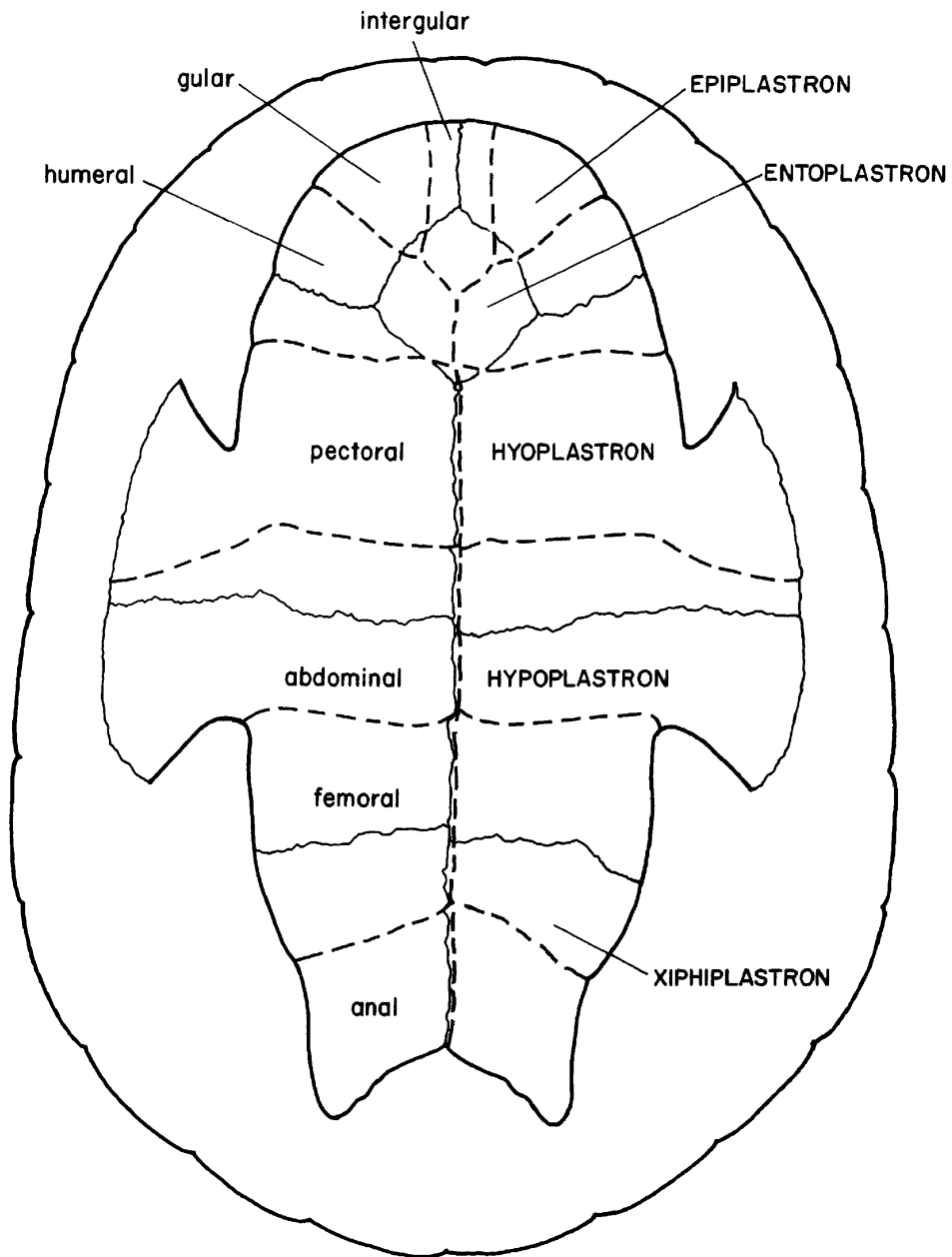
FIG. 14. Ventral view of plastron, *Emydura* sp., UCMP 77348, Wipariji Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia. Partial restoration, bones labeled on right side of figure, scutes labeled on left side of figure.

as lacking neurals, Rhodin and Mittermeier (1977) have recently shown that they occur as variants in Recent *Chelodina* and *Emydura* *(Elseya)*, whereas *Chelodina oblonga* consistently has neurals (Burbidge, Kirsch, and Main, 1974). I have hypothesized elsewhere (Gaffney,

FIG. 15. Dorsal view of carapace, *Emydura* sp., UCMP 72492, Wipariji Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia.

1977, p. 18) that the complete absence of neurals may be a primitive feature of the Chelidae and the possession of them in the tribe Chelini (*Phrynops, Chelus, Chelodina,* and *Hydromedusa*) may be a derived feature for that group alone. The general absence of neurals in the fossil Australian chelids neither supports nor contradicts this idea.

*Emydura (Elseya) dentata* and *E. latisternum* are usually characterized (at least in the

FIG. 16. Ventral view of plastron, *Emydura* sp., UCMP 72492, Wipajiri Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia.

young) by a serrated posterior margin of the shell. Although UCMP 72492 appears to have a serrated margin, this condition seems to be due to breakage along the peripheral sutures. In any case, *Emydura dentata* has serrations that

are indented along the contact between scutes, whereas the indentations in UCMP 72492 occur along sutures.

The two Wipajiri shells agree closely with each other in all preserved features except two:

overall size and the shape of vertebral scutes 3
and 4. UCMP 77348 is large for a chelid (the
South American *Chelus* exceeds it), possibly
the largest Australian chelid known at present.
Measured in a straight line along the midline it
is 44.5 cm. in length, whereas UCMP 72492 is
36 cm. long. The largest *Emydura* shell re-
ported by Goode (1967, p. 81) is 29.2 cm. in
length and the largest Australian chelid shell
noted by Goode (1967, p. 38) is a *Chelodina
expansa* of 42.3 cm., which is close in size to
the Wipajiri shell.

The sulcus between the third and fourth ver-
tebral scutes on UCMP 72492 differs markedly
from any other *Emydura* that I have seen. In-
stead of being straight, an anterior lobe of the
fourth vertebral extends into the area occupied
by the third vertebral in other *Emydura*. Al-
though this lobe is symmetrical and the shell
gives no indication of abnormality in this area,
I am not considering this feature to be of sys-
tematic significance. In any case, this sort of
feature is not characteristic of any other chelid
taxon that I am aware of and would only serve
to separate UCMP 72492 as the sole member
of a new taxon. The other Wipajiri shell does
not have this feature.

PLASTRON: As is the case with the carapace,
the plastron of the Wipajiri shells agrees
closely with Recent *Emydura* and can be read-
ily differentiated from *Chelodina* and *Pseude-
mydura*. *Chelodina* and *Pseudemydura* are
unique among chelids in having a large intergu-
lar scute that entirely separates the humeral
scutes and contacts the pectorals. Also,
Chelodina is unique among chelids in having
the gular scutes meet anterior to the intergular
thereby separating the intergular from the ante-
rior edge of the shell. The Wipajiri shells have
a narrow intergular that separates the gulars and
only part of the humerals as in *Emydura*. In
fact, the intergular is particularly narrow, being
almost three times longer than wide (based pri-
marily on UCMP 77348 but agreeing with
UCMP 72492 to the extent that the latter is
preserved). A narrow intergular is a character
commonly found in *Emydura (Elseya) dentata*
(Goode, 1967; Cogger, 1975).

3. CERVICAL VERTEBRAE

Although none of the vertebrae from V 5762

can be associated with each other, it is possible
to identify the position of many of the cervicals
within certain limits. The family Chelidae have
a unique pattern of centrum articulations,
namely (2(, (3(, (4(, (5),)6),)7(, (8) according
to Williams (1950). On the basis of this pattern
(and zygapophysis position for cervical 2), the
following categories can be identified: second,
third or fourth, fifth or eighth, sixth, and sev-
enth cervicals. All of these categories are repre-
sented by specimens except for the seventh
cervical.

In my earlier chelid paper (1977) I used only
one cervical feature: cervical vertebrae longer
than dorsal vertebrae as a synapomorphy for
the subtribe Chelina *(Chelus, Chelodina, Hy-
dromedusa)*. As there are no associated dorsals
available for these cervicals to be compared
with, this criterion does not help much.
However, in that paper I neglected an impor-
tant study by Kasper (1903) on the cervical
vertebrae of pleurodires (see also Hoffstetter
and Gasc, 1969, p. 210). Kasper divided the
chelids into four groups based on atlas-axis
morphology using features that can readily be
interpreted as synapomorphies. Kasper's groups
are as follows:

   I. *Rhinemys nasuta (=Phrynops nasuta)*
      Elseya latisternum
  II. *Hydraspis hilarii (=Phrynops geof-
      froanus)*
      Chelus fimbriata
 III. *Chelodina longicollis*
 IV. *Hydromedusa maximiliani*
      Platemys platycephala

Group I has the primitive condition for the
features used by Kasper and he argued this in a
very "cladistic" way by showing that they oc-
cur outside of chelids in pelomedusid pleuro-
dires and in most cryptodires. Group II, III,
and IV are progressively advanced and I inter-
pret these as follows: Groups II and III and IV
are characterized by an atlas that is more than
half as long as the axis (the primitive condition
is an atlas that is less than half the axis length)
and an atlas intercentrum that is relatively small
in comparison to the rest of the atlas (the prim-
itive condition is a relatively large atlas inter-
centrum). Groups III and IV are characterized

by axis-atlantal zygapophysis articulations that are horizontal (rather than somewhat vertical, the presumed primitive condition) and by the development of close fitting sutures (or complete fusion) of the neural arches and centrum of the atlas (rather than the relatively more open condition in other turtles).

Much of Kasper's taxonomy parallels my hypothesis of chelid phylogeny; for example: Groups II and III and IV of Kasper have nearly the same content as my infrafamily Chelodd (with the exception of *Phrynops nasuta*, discussed below), and his Groups III and IV are distinctly at variance with my hypothesis because Kasper would place *Platemys, Hydromedusa,* and *Chelodina* together while I have argued that *Platemys* is relatively more primitive and that *Phrynops, Chelus, Chelodina,* and *Hydromedusa* form a monophyletic group with *Platemys* as its sister taxon. Much to my surprise, an examination of specimens strongly suggests that Kasper misidentified the cervicals of *Platemys.* Kasper's figures of the cervicals of *"Platemys"* and *Hydromedusa* (Kasper, 1903, figs. 10, 11) show vertebrae that are nearly identical with each other, *"Platemys"* differing only in being slightly smaller and having a closely attached but unfused atlantal intercentrum. The specimens I have seen of *Platemys* (specimens including skull and shell so that correct identification is assured), however, show cervicals that lack all the features indicated by Kasper for Groups II, III, and IV. *Platemys* has the primitive condition for the characters used by Kasper, namely, the atlas is about one-half the length of the axis, the atlantal intercentrum is relatively small, the axis-atlas zygapophyseal articulations are more vertical, the atlantal elements (neural arches, intercentrum, and centrum) are not fused but are loosely articulated. In general, the cervicals of *Platemys* are quite similar to those of *Emydura.* It seems to me that Kasper may have used a small specimen of *Hydromedusa* that was misidentified as *Platemys.* I base this suggestion on the very close agreement of the cervicals of *"Platemys"* and *Hydromedusa* in his figures and on his statement (p. 160) that the skulls of *Hydromedusa* and *Platemys* are nearly identical. In fact, the skulls of these two

taxa are quite different (see Gaffney, 1977, figs. 2-5), *Platemys* having a relatively broad temporal roof and *Hydromedusa* having virtually none at all.

With this apparent error rectified, it can be seen that Kasper's Groups III *(Chelodina)* plus IV *(Hydromedusa)* are the same as my infratribe Hydromedusad. Another difference between Kasper's scheme and mine is his placement of *Hydraspis* with *Chelus* as a more advanced group than *Rhinemys.* I have put both *Hydraspis* and *Rhinemys* in the same genus, *Phrynops,* but I noted (1977, p. 10) that *Phrynops* might be paraphyletic. Kasper's characters might allow one to discriminate taxa within such a paraphyletic *Phrynops,* in which case *P. geoffroanus* would be a member of a monophyletic group containing it and the subtribe Chelina. Unfortunately, I have seen no cervicals of *Phrynops* and can only advance this idea for future work.

From the fossil turtle material from Lake Palankarinna, it can be seen that cervical vertebrae of chelids can provide quite useful information. Virtually any cervical can be distinguished between *Chelodina* and *Emydura,*[1] and a member of the tribe Chelini may be identified by the atlas–axis. The Palankarinna material contains a number of cervicals but the most important for my purposes are three atlas neural arch halves and four axes. These elements, although not associated with each other, show the primitive chelid condition as seen in Recent *Emydura,* with no indication of the features seen in the subtribe Chelina. The atlas neural arches have sutural connections dorsally but the ventral connections with the centrum and intercentrum are flat and uncomplicated. Similarly, the axis and remaining cervicals agree closely with Recent *Emydura.*

4. LIMB MORPHOLOGY

The only articulated limb material from an Australian chelid was found associated with UCMP 72492 at the Lake Ngapakaldi Leaf Locality (V 6213). The specimen consists of a shell (figs. 15, 16, discussed above) with variably preserved portions of all four limbs. No

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[1]*Pseudemydura* is rare and I have not examined its cervicals so I cannot add this taxon to my comparisons.

vertebrae or cranial elements are present. The forefeet are the best preserved and consist of nearly all the elements. They were apparently articulated originally but during preparation they were reassembled in such a way that many of the phalanges and metacarpals are not in their natural position. The carpus of each foot is still in articulation, and as left and right agree I have used this without modification in figure 17. The radius and ulna of the left side are complete and also used (after reversal) in this figure. The metacarpals and phalanges are not readily restored, however, and I have only used the proximal parts of the metacarpals based on Recent *Emydura* for position in this figure.

The carpus of chelids is poorly known in the literature; the only figures I have found are in Hoffman (1890, plate IX, figs. 10, 11, *Chelodina* and *Emydura*, respectively). Although my sample is very small, it appears that *Chelodina* consistently differs from *Emydura* in that distal carpals 5, 4, and sometimes 3 fuse in *Chelodina* but do not in *Emydura*. I do not know the distribution of this feature in other chelids. The Wipajiri specimen has no carpal fusion and is very similar in all aspects of its morphology to Recent *Emydura*.

Both hind feet are present but although parts of the digits are articulated neither tarsus is well enough preserved to allow a complete restoration. In its preserved parts it agrees with *Emydura*.

Some disarticulated appendicular and vertebral elements identifiable as turtle or chelid are known from V 6213 and V 5762. All of this material is more or less fragmentary but the preserved elements are consistent with *Emydura*.

DISCUSSION

The cranial material from the Etadunna Formation at Lake Palankarinna is the best-preserved fossil cranial material of chelids that has yet been found. All the material from this locality (V 5762) is consistent with the presence there of only one chelid taxon, and this taxon can be identified with the Recent genus *Emydura* as delimited in Gaffney (1977), that
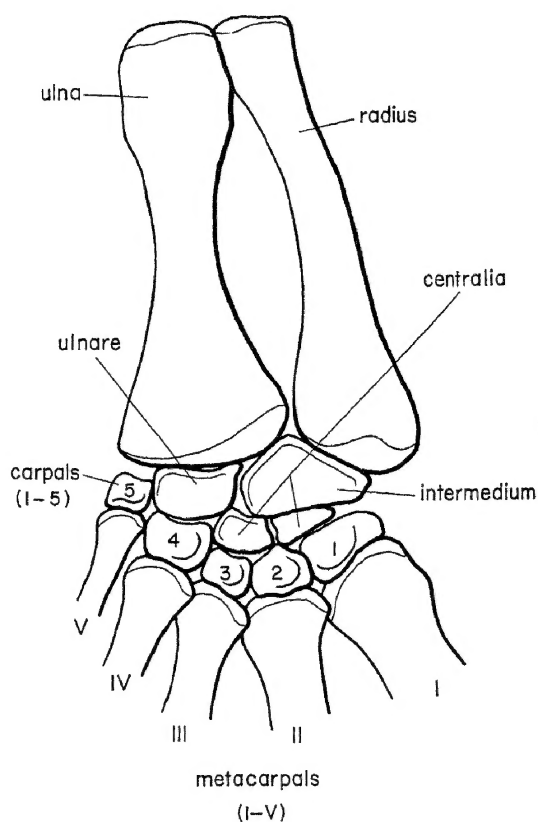

FIG. 17. Dorsal view of partially restored right forefoot, *Emydura* sp., UCMP 72492, Wipajiri Formation, Miocene, V 6213, Lake Ngapakaldi, South Australia.

is, to include *Elseya*. However, identification of this fossil taxon as *Emydura* must be qualified. In my review of chelids (1977, p. 5) I concluded that the assemblage of species currently placed in *Emydura* (including *Elseya*) was not a well-tested monophyletic group. The only feature unique to *Emydura* that is not primitive for the Chelidae is the relatively heavy lower jaws with moderate symphyseal "hook," but this character also occurs in pelomedusids and may turn out to be primitive for chelids. Furthermore, the V 5762 collection contains no lower jaws, although one has been found at V 6213.

Nonetheless, the Etadunna skulls can still be placed rather precisely in the phylogenetic hypothesis I have presented earlier (1977). The Etadunna specimens have an anterior frontal

process at least partially separating nasals (see Frontal for discussion), which is a derived character for the subfamily Chelinae, but they lack the derived features (dorsal processes of exoccipitals meet medially above foramen magnum) of the infrafamily Chelodd. *Emydura* is the only taxon that occupies this phylogenetic position in my hypothesis (1977, p. 17, fig. 10), and in the absence of any diagnostic differences between the Etadunna skulls and Recent *Emydura*, I identified the fossil forms with this taxon. The question remains, however, of *Emydura* monophyly, and I do not propose to answer it here. When a rigorous test of *Emydura* monophyly is available then more detailed comparisons of the Etadunna material with Recent *Emydura* species can be made. Until that time, I refer to the Etadunna chelid as *Emydura* sp. even though this taxon may very well be paraphyletic. The shells and other postcranial material are less definitive but can still be identified as *Emydura* sp.

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